SURVEY OF CHROMOSOME NUMBERS IN *RUBUS* (ROSACEAE: ROSOIDEAE)[1]

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ABSTRACT

A literature survey was made of chromosome number counts for *Rubus* species. Numbers are presented for 387 species, representing about 40 percent of the total number, and including 11 of the 12 subgenera. The basic number is universally 7 and ploidy levels include 2*x*, 3*x*, 4*x*, 5*x*, 6*x*, 8*x*, 9*x*, 10*x*, 11*x*, 12*x*, 14*x*, and, questionably, 13*x* and 18*x*. In a few species, more than one chromosome number has been reported. Attempts were made to provide the currently accepted taxonomic designation for each species as well as the outdated synonyms used in original publications. The objective was to provide a summary of available information on chromosome numbers of *Rubus* species and to point out the gaps that need to be addressed.

Rubus is a large and important genus that includes an estimated 900 to 1000 species widely distributed throughout the world. Representatives are found on all arable continents as well as on oceanic islands, and many species provide an important food resource for both humans and animals. Early cytological studies demonstrated that polyploidy has played a significant role in the evolution of this genus (Gustafsson, 1943). The basic number is universally 7 and, currently, ploidy levels are known to range from 2*x* to 14*x*, and possibly 18*x*. The most recent survey of *Rubus* chromosome numbers was included in *Chromosome Numbers of Flowering Plants* (Fedorov, 1969). Since that time, counts for many more *Rubus* species have been published in widely scattered reports. Knowledge of the chromosome numbers of species is important to botanists studying cytotaxonomy, evolution, and phylogenetic relationships and to plant breeders utilizing interspecific hybridization as a breeding procedure.

The exact number of species is unknown because the only comprehensive world taxonomic treatment was published more than 80 years ago (Focke, 1910–1914). During the past eight decades, many new species have been described and, as new evidence has accumulated, many nomenclatural changes made. Recent regional taxonomic studies such as those by Davis (1990), Davis et al. (1967–1970), Edees and Newton (1988), Hogdon and Steele (1968), Kalkman (1984, 1987), Weber (1972, 1981), Weber and Maurer (1991), Yü (1985), and Zandee and Kalkman (1981) have helped clarify the identity of many species in the authors' respective regions. Excluding the subgenus *Rubus*, there are approximately 335 species. For subgenus *Rubus* in Europe, Edees and Newton (1988) gave 300 species in Britain alone (not including the numerous continental species), whereas for this subgenus in eastern North America, Davis (1990) claimed 198 species. Thus, current estimates of the total number of species in the genus *Rubus* may reach 900 to 1000. A comprehensive taxonomic study of this genus is needed to determine more accurately the number of species.

Chromosome number counts for 387 species, representing about 40 percent of the species in the genus, are presented in Table 1, at the end of this article. An additional 75 taxa in subgenus *Rubus* whose names are invalid or whose identities are uncertain are also given because, although not accurately named, they are representatives of the European blackberry flora. Although voucher specimens are reportedly available for some of the species counted, I have made no effort to verify their identity, except for those counted by myself. However, by consulting recent literature and through personal communication with taxonomists specializing in *Rubus*, I have attempted to provide currently accepted names for the species reported. The originally published name is also included so that, in the event that my re-naming is incorrect, a *Rubus* taxonomist could readily identify the species. The number of counts for a species varies from

[1] The author gratefully acknowledges the assistance of the following *Rubus* specialists who kindly reviewed specific subgenera and made valuable nomenclatural suggestions in the early stages of preparation of this manuscript: Heinrich E. Weber for the European blackberries; Mark Widrlechner for North American blackberries; and Naohiro Naruhashi for the subgenus *Ideaobatus*.

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one to several. In cases where different chromosome numbers are reported for a species, these may be explained by one of the following: one of the counts may represent a variant individual resulting from spontaneous doubling of chromosomes at some early stage of development or from the union of an unreduced gamete with a reduced gamete, a common phenomenon in this genus; they may actually represent populations within a species that have different ploidy levels; or they may be the result of mistaken identification by an author.

In the discussion and in Table 1, the species, chromosome numbers, and reference citations are arranged according to the subgenera established by Focke (1910–1914), except for *Micranthobatus*, whose species have been separated out of *Lampobatus* by Kalkman (1987), and *Dalibarda*. Since most of the species placed in subgenus *Dalibarda* by Focke (1910–1914) have been transferred to subgenus *Cylactis* and *R. dalibarda*, itself, has been moved to a different genus, as *Dalibarda repens* L. (Bailey, 1941), the continued acceptance of *Dalibarda* as a subgenus is questionable. In Table l, the currently accepted name is given first, synonyms are indented under the valid name, and names indented, in parentheses, and preceded by "as" indicate that in the original publication, identification was incorrect but, subsequently, the plant was reidentified. Eleven of the 12 subgenera are represented: only *Lampobatus* sensu stricto remains to be studied.

Subgenus *Chamaemorus*

The chromosome number of *R. chamaemorus*, the only species in this subgenus, is well established with 18 hexaploid counts.

Subgenus *Chamaebatus*

Of about six species in this subgenus, three have been counted: *R. calycinus* and *R. pectinellus* are hexaploid, whereas *R. nivalis* is diploid.

Subgenus *Comaropsis*

Only one of the two species in this subgenus has been counted: *R. geoides* is tetraploid.

Subgenus *Cylactis*

There are chromosome number counts for 10 of the appproximately 16 species now included in this subgenus. Six of these, *R. lasiococcus*, *R. pedatus*, *R. pubescens*, *R. pseudojaponicus*, *R. stellatus*, and *R. subarcticus* are diploid. *Rubus arcticus* which, with several counts, is no doubt predominately diploid, was found to have a distinct triploid population (Johnson & Packer, 1968). Zhukova (1980) also reported triploidy for this species. It is not uncommon that diploid species give rise to an occasional triploid or tetraploid individual which may, through vegetative reproduction or apomictic seeds, spread to form colonies or populations of considerable extent. In the case of *R. humulifolius*, more information is necessary to determine whether this species is mainly diploid (two counts) or tetraploid (one count). However, for *R. nepalensis*, the three tetraploid counts, as compared to only one diploid, suggest that it may be principally a tetraploid species. With 14 counts, *R. saxatilis* is well established as a tetraploid species.

Subgenus *Orobatus*

Of the approximately 18 species in this exclusively South American subgenus, 6 have been counted and all are hexaploid. These include the relatively weak-growing plants of *R. acanthophyllus*, *R. coriaceus*, and *R. glabratus*, as well as the very vigorous species *R. macrocarpus*, *R. nubigenus*, and *R. roseus*, which is also vigorous and has robust canes to 6 m or longer. This high chromosome number contrasts with the consistent diploid number in the blackberries (subg. *Rubus*) that occur in the same Andean region as the *Orobatus* species.

Subgenus *Dalibardastrum*

Three of the 10 to 12 species in this subgenus have been counted and all are polyploid; *R. tricolor* and *R. tsangorum* are tetraploid, whereas *R. amphidasys* is hexaploid.

Subgenus *Malachobatus*

When Fedorov (1969) published his *Rubus* chromosome number survey, only seven species in the *Malachobatus* had been counted. Currently, 40 (31%) of the estimated 127 species have been counted. Thus far, all species in this subgenus are polyploid: there are twenty-seven 4*x*, five 6*x*, six 8*x*, and two 14*x* species. Although there are seven diploid counts, this ploidy level is not consistent with other information. Four of the species reportedly diploid were found to be high polyploids by other investigators: *R. fairholmianus* was octoploid (Nybom, 1986); *R. gardnerianus* was octoploid (Gill et al., 1984; Singhal et al., 1990); *R. rugosus* was both octoploid (Iwatsubo & Naruhashi, 1992) and 14*x* (Nybom, 1980, 1986; Thompson, 1995a); and *R. hayata-koidzumi* was tetraploid (Iwatsubo & Na-

ruhashi, 1993; Thompson & Zhao, 1993). Of the other three doubtful diploid species, two have sole counts, namely, *R. fulvus* and *R. micropetalus* by Subramanian (1987), and the third, *R. paniculatus*, has two counts (Malik, 1965; Mehra & Dhawan, 1966). The identity of all species with diploid counts needs to be verified and their counts reconfirmed before it can be concluded that diploid species occur in this predominately polyploid subgenus.

Omitting the discrepant diploid counts, there appear to be three species in which two different numbers actually do occur. Naruhashi and Iwatsubo (1993) reported that two forms, both hexaploid and octoploid, are commonly found in both *R. hakonensis* and *R. buergeri*. For *R. rugosus*, there is one octoploid and three 14*x* counts. These two different counts for *R. rugosus*, along with the ploidy levels reported for its close relative, *R. moluccanus* (4*x*), and *its* allies *R. multibracteatus* (4*x*), *R. hillii* (6*x*), *R. fairholmianus* (8*x*), possibly *R. indicus* (8*x*), and *R. glomeratus* (14*x*), suggest that this group of species represents a polyploid complex. Further cytotaxonomic studies are necessary to clarify the relationships among these species.

Thus far, there is no evidence for apomixis among the *Malachobatus* polyploid species. Nybom's (1986) demonstration of sexual reproduction in two species, *R. fairholmianus* and *R. rugosus*, needs to be expanded to other species in order to determine if this is the predominate mode of reproduction in this subgenus. The existence of relatively clear-cut species boundaries supports the concept that hybridization and apomixis have not played an important evolutionary role, if any, as they have in *Rubus*, the other major polyploid subgenus.

Subgenus *Anaplobatus*

In this small subgenus of possibly five to six species, the four species counted are all diploid. *Anoplobatus* is closely related to the predominately diploid *Idaeobatus*. The sole triploid report for *R. deliciosus* by Longley (1924) was no doubt an aberrant individual or possibly an interspecific hybrid.

Subgenus *Idaeobatus*

Counts have been reported for 70 (52%) of the estimated 135 species in this subgenus. Fifty-five of these are reported only as diploids; nine of them are reported as both diploid and other ploidy levels; four are reported as tetraploid only; one as ca. 13*x*; and one as 18*x*. The nine species that are reported as diploid plus other counts are probably basically diploid, with the other counts, triploid or tetraploid, merely cytological aberrant individuals or colonies. The single triploid count for *R. strigosus*, which is a well-established diploid species, as well as the sole triploid counts for the diploid species *R. parvifolius* and *R. yoshinoi*, represent aberrant individuals which arose from union of a reduced and an unreduced gamete (Naruhashi & Iwatsubo, 1993). Spontaneous chromosome doubling in zygotes or in somatic tissues to form tetraploid individuals is also not uncommon. The tetraploid counts for the basically diploid species *R. foliolosus*, *R. hypargyrus*, and *R. niveus* are most likely aberrant individuals of this type. The chromosome numbers above diploid reported for the South African species *R. apetalus* (2*x* and 4*x*), *R. longipedicellatus* (2*x*, 4*x*, and 5*x*), and *R. pinnatus* (2*x* and 4*x*) have been explained by Spies and DuPlessis (1985) as having arisen through interspecific hybridization and introgression, accompanied by doubling of chromosomes. The primary basic number for these species is considered to be diploid. Altogether, it appears that 63 (90%) of the 70 *Idaeobatus* species counted are basic diploid species.

The four species for which only tetraploidy has been reported include *R. leucocarpus*, *R. nishimuranus*, *R. probus*, and *R. sachalinensis*. These species arose recently enough that their progenitors have, with a certain degree of certainty, been ascertained or can be postulated. With no knowledge of the chromosome number, Focke (1910–1914) considered *R. leucocarpus* to be a subspecies of *R. niveus* Thunb. and mentioned that it differs from the typical species in its larger flowers and fruits and its more robust plant, traits that are characteristic of autotetraploids. Thus, it is probable that this species arose directly from *R. niveus*. The suspected hybrid origin of the tetraploid *R. nishimuranus* has been confirmed by Naruhashi (1976) and Naruhashi and Iwatsubo (1993), who concluded that this species is an allopolyploid derived from a cross of *R. trifidus* × *R. hirsutus*. The third tetraploid *Idaeobatus* species, *R. probus*, was recently reported (as *R. muelleri*) by Thompson (1995a), who made counts on three plants from Australia; two plants from one source and one plant from another. Because this species is so similar to *R. fraxinifolius*, Australian botanists have disagreed as to whether it should be included in that species or considered a separate species. The tetraploid count of *R. probus* provides another trait, in addition to minor morphological traits, that may help to distinguish these two species; that is, if *R. fraxinifolius* is diploid, as suspected. It is not possible to claim, although in-

teresting to speculate, that *R. probus* may be an autopolyploid derivative of *R. fraxinifolius*. The fourth tetraploid *Idaeobatus* species, *R. sachalinensis*, which is widely distributed in northeast Asia, was demonstrated by Rozanova (1939) to have arisen through autopolyploidy from *R. idaeus*. In northeast Asia, *R. idaeus* varieties *melanolasius* and *sachalinensis* (both now included in *R. sachalinensis)* are tetraploid. However, the forms to which these varietal names have been applied in northwestern North America (included here as synonyms of *R. strigosus*) are diploid. Although not given in Table 1, several polyploid raspberry cultivars (*R. idaeus*) have arisen spontaneously, e.g., the triploid 'November Abundance', 'Belle de Fontenay', and 'All Summer' (Darrow, 1937) and the tetraploid 'Colossus', 'Hailshamberry', and 'LaFrance' (Jennings, 1988).

The most puzzling reports for this almost universally diploid subgenus are the very high ploidy counts reported for two *Rubus* sp. in the mountains of New Guinea by Borgmann (1964). Fortunately, Borgmann (1964) cited voucher specimens for these unknown *Rubus* species and C. Kalkman, of the Rijksherbarium in Leiden, the Netherlands, very kindly provided me with the identification of these as well as Borgmann's (1964) other unknown species with chromosome counts (C. Kalkman, pers. comm.). The *Idaeobatus* species are *R. archiboldianus* ($2n$ = ca. 91) and *R. lorentzianus* ($2n$ = 126). Both of these counts are highly suspect. Zandee and Kalkman (1981) mentioned only nine *Idaeobatus* species in New Guinea. Based on their relationships, six of these would be expected to be diploid; *R. fraxinifolius* and *R. chrysogaeus* are related to *R. rosifolius* ($2x$); and *R. ferdinandi-muelleri*, *R. papuanus*, and *R. montis-wilhelmi* ($2x$) are closely related enough to be considered a species complex. The chromosome number for the ninth species, *R. macgregorii*, has not been reported. These extraordinarily high chromosome numbers definitely need confirmation, as well as counts made for the other species in New Guinea, before an attempt can be made to hypothesize how two species with such high ploidy levels of $13x$ and $18x$ could have evolved from the surrounding species that are most likely diploids. It is possible that cytological preparations of these *Rubus* sp. may have been mislabeled. If the count really was of a *Rubus* species, this high number may belong to an unknown *Malachobatus* species because polyploidy is common in this subgenus, with levels reaching $14x$ ($2n$ = 98).

Subgenus *Micranthobatus*

Of about 12 species in this subgenus, chromosome numbers have been counted for 5: *R. cissoides*, *R. parvus*, *R. schmidelioides*, and *R. squarrosus* from New Zealand and *R. royenii* var. *hispidus* from New Guinea are all tetraploid.

Subgenus *Rubus* (European blackberries)

The major challenge in this subgenus is not cytological but rather taxonomical. For over 200 years, and continuing today, numerous taxonomists have described and named a few thousand species in this very complex group. The massive array of variation that exists results from the reproductive processes characteristic of this group. Except for the few sexual diploid species, most species are facultative apomicts that can freely hybridize, even with rather distantly related species. In addition to sexual reproduction, segregating offspring may arise through a subsexual process involving normal meiosis in the embryo sac, followed by fusion of two of the resultant haploid cells. However, the predominate mode of reproduction is pseudogamy. Although pollination is necessary to initiate development, the embryo is strictly maternal, which provides a mechanism for wide distribution of a uniform genotype. In this subgenus, there is an equilibrium system in succeeding generations with alternating apomictic and sexual reproduction, which provides for both segregation and rapid, extensive dispersal of a single genotype. Depending upon its adaptability, this "clone" may occur as a local variant in a limited area only or it may become very widespread, thus simulating a true species. Dispersal is accelerated further by the universal propensity for vegetative propagation. These processes have combined to cause a blurring of conventional species boundaries, which accounts for the numerous nomenclatural discrepancies among taxonomists and the thousands of names that have been proposed and subsequently discarded. Although there are some species that are widely distributed and morphologically distinct enough to be recognized by all botanists, there are many more forms where boundaries are not so clear-cut. It is unlikely that an exact number of species will ever be universally accepted.

Plants with aberrant chromosome numbers may arise through parthenogenesis to give haploid plants, by meiotic disturbances that result in aneuploids, from unreduced gametes that give rise to offspring with increased chromosome numbers, or by spontaneous doubling of chromosomes in somatic cells.

Many of the chromosome counts presented in Table 1 were made many years ago when a different classification and nomenclatural system was in vogue. Heslop-Harrison's (1953) major cytological study of this group relied upon the species designations of W. C. R. Watson, the authority for British *Rubus* taxonomy at that time (Watson, 1958). Subsequently, Edees and Newton (1988) reassessed this genus in Britain and have discarded, for various reasons, many species names applied by Watson. Therefore, many of Heslop-Harrison's chromosome counts were made on taxa whose identity is now questionable. Gustafsson (1943) summarized his and others' counts for European blackberries and, although some of his Scandinavian species have been revised, in several cases the current synonymy is known so the counts can be presented for validly named species. In other cases, names were applied to local forms without proper documentation; these have been relegated to uncertain identity or invalid species names. Principal authorities used to establish current nomenclature in the European blackberries were Weber (1972), Weber (1981), H. E. Weber (pers. comm.), and Edees and Newton (1988), although I take full responsibility for all errors in interpretation.

Chromosome numbers are reported here for 194 species of European blackberries with my concept of currently accepted nomenclature (while recognizing that there may not be general agreement among taxonomists about these names). Since the cytological situation differs somewhat in the two major sections of this subgenus in Europe, they will be treated separately.

In section *Rubus*, chromosome counts of 154 species are summarized. Only three (2%) basic diploid species have been documented; *R. canescens*, *R. ulmifolius*, and its close relative, *R. sanctus*.

Six (4%) species are reported to be triploid; *R. divaricatus* (as *R. nitidus* complex), *R. grabowskii* (as *R. thrysoideus* complex) and its close relatives, *R. elatior* and *R. montanus*, are all well established as triploid species (Gustafsson, 1943). The sole count of tetraploid for *R. divaricatus* is either an error or an aberrant individual. *Rubus brevistaminosus* and *R. hylophilus*, with only one triploid count each, need confirmation.

With 125 species counted only as tetraploid, this is clearly the predominate ploidy level in this section. Intraspecific chromosome number variation is reported for 14 species, all of which have at least one tetraploid count. The one diploid count in *R. infestisepalus* was interpreted by Heslop-Harrison (1953) to be a haploid variant in this tetraploid species. The triploid count for *R. fissus*, reported by Beijerinck (1956), was made on a single plant and contrasts with the other tetraploid counts for this species. *Rubus leucostachys*, with one triploid count and one tetraploid, remains to be clarified. Six species are given as both tetraploid and pentaploid; *R. drejeri*, *R. formidabilis*, *R. hartmanii*, *R. lentiginosus*, *R. milesii*, and *R. pedemontanus*. Except for *R. pedemontanus*, the chromosome numbers of these species need to be reappraised. Although Gustafsson (1943) considered *R. pedemontantus* (as *R. bellardii*) to be a uniform, widespread, and well-established pentaploid species and dismissed the tetraploid count in Maude (1939) as an error, two additional tetraploid counts have been subsequently reported. Czapik (1987) specifically mentions two chromosome races for *R. bellardii* in Europe. Also, it may be that the two different counts given for *R. pedemontanus* can be accounted for by the fact that *R. bellardii* is synonymous only in part with *R. pedemontanus* and that I have erroneously synonymized all *R. bellardii* reports. Four species are reported as both tetraploid and hexaploid: *R. infestus*, *R. newbridgensis*, *R. nitidiformis*, and *R. pyramidalis* var. *parvifolius*. Heslop-Harrison (1953) explained that the hexaploid count for *R. pyramidalis* var. *parvifolius* was clearly an aberrant seedling, probably resulting from an unreduced gamete, because determinations from the adult plant were all tetraploid. It is possible that a similar explanation may account for the single hexaploid counts for *R. infestus*, *R. newbridgensis*, and *R. nitidiformis*. In the absence of any well-established hexaploid species in this section, it is most likely that the primary number for all species where these two different counts are given is basically tetraploid and that other counts are due to occasional aberrant plants or to errors in identification. Additional counts are necessary to verify this supposition. Altogether, if species with both tetraploid and other counts (except for the triploid *R. divaricatus*) are added to those with only tetraploid counts, 139 of the 154 (90%) of the species in this section are tetraploid.

Five (3%) of the species are reported to be pentaploid: *R. anglocandicans*, *R. marshallii*, *R. kollundicola*, *R. pedemontanus*, and *R. vestervicensis*. There are only single counts for the first two species and, in fact, Heslop-Harrison (1953) suspected that the single plant of *R. marshallii* counted was actually a large form, not typical of the species. Thus, these two species need confirmation. The other three have been well documented by Gustafsson (1943) as pentaploid. Of these pentaploid species, only *R. pedemontanus* is widely distributed in Eu-

rope; the others are local endemic forms in Britain and in Sweden.

The only hexaploid count for a species in the section *Rubus* is a single count for *R. bloxamianus* in Maude (1939) which, without confirmation, may be considered an aberrant individual or an error. Both Gustafsson (1943) and Heslop-Harrison (1953) concluded that, except for a possible aberrant individual, hexaploid species are not found in this section. This conclusion has been substantiated in subsequent studies.

In section *Corylifolii*, as in section *Rubus*, tetraploidy is the predominate chromosome number. However, this section differs cytologically in several respects: there are no diploid species, there are relatively more pentaploid species, there are a few hexaploid species, a few species have two cytotypes, and there are a few aneuploids.

The lack of diploids is to be expected since Lidforss (1914) postulated that species in this section were primary and secondary hybrids and segregation products of crosses between the tetraploid *R. caesius*, a species currently placed in its own, monotypic section, *Caesii*, and species in section *Rubus*. The *Corylifolii* species are not as numerous nor as widely distributed as species in section *Rubus* and species boundaries are even less distinct, as evidenced by the relatively large number of varieties described for some species (Gustafsson, 1939).

Of the 38 species counted, 17 (45%) are given as tetraploid only and 8 (21%) as pentaploid only. Four (10%) are well documented as hexaploid only. The fact that the hexaploid species are few in number and have rather limited distribution suggests that this ploidy level is not well developed. Gustafsson (1939) presented evidence that in nine (24%) of the *Corylifolii* species, populations do occur with different chromosome numbers. His results are creditable not only because of his knowledge of the species identity, but also because he made several counts on samples from different populations. *Rubus camptostachys* was 4*x*, 6*x* and aneuploid (± 30); *R. dissimulans* varieties were 4*x*, 6*x* and aneuploid (± 42); *R. eluxatus* was 4*x* and aneuploid (± 28 and 6*x* + 3); *R. fasiculatus* was 4*x*, 5*x*, 6*x*, and aneuploid (4*x* + 1); *R. gothicus* was 4*x*, 5*x*, and ± 28; *R. lidforssii* was 4*x* and 5*x*; *R. lindbloomii* was 4*x* and 6*x*; *R. nemorosus* was 4*x* and 5*x*; and *R. norvegicus* was 4*x*, 5*x*, and 6*x*. The counts of both tetraploid and hexaploid reported for *R. conjungens* by Heslop-Harrison (1953) were not explained as representing different populations, so it is not clear if the hexaploid count reflects a different cytotype or merely an aberrant individual.

Counts for 75 "species" in both sections *Rubus* and *Corylifolii* classified as "doubtful determination and/or taxonomic status" are presented here, but separately because, regardless of their true identity, these data add to the cytological picture of the group as a whole in Europe. These include many counts for British plants to which valid continental species' names had been erroneously applied, local forms that had originally been given species rank but are no longer accepted as such, aggregate species such as *R. hirtus*, as well as forms to which names were applied but never documented.

Subgenus *Rubus* (North American Blackberries)

Chromosome numbers in the North American blackberries were studied most intensively in the East by Longley (1924) and Einset (1947), and in the West by Fischer et al. (1941), Darrow and Longley (1933), Brown (1943), and Zielinski and Galey (1951). In comparing the blackberries of eastern North America with those of Europe, some similarities and differences may be mentioned. One similarity is the important evolutionary role of interspecific hybridization and facultative apomixis so that species boundaries are difficult, if not impossible, to define accurately. Another commonality is the significance of polyploidy in speciation, although the eastern North American group represents an even wider range of ploidy levels, including 2*x*, 3*x*, 4*x*, 5*x*, 6*x*, 7*x*, 8*x*, 9*x* and even one aneuploid (5*x* + 1) species. Also similar is the common association of facultative apomixis (pseudogamy) with polyploidy (Einset, 1951). One significant difference is the existence of several, apparently sexual, diploid species compared to only three diploids among the several hundred species of blackberries in Europe. Also, whereas tetraploid is the dominant ploidy level in the European blackberries, this number appears to be relatively less common in the North American species. From the limited counts available for eastern North American species, it appears that, except for the section *Flagellares* where ploidy levels higher than tetraploid are common, the most frequent numbers reported are diploid and triploid.

The most recent attempts to clarify the taxonomy of the eastern North American blackberries were those of Davis et al. (1967–1970), updated by Davis (1990), and Hogdon and Steele (1968). Species listed in Table 1 follow the Davis et al. (1967–1970) treatment (with modifications suggested by Mark Widrlechner, pers. comm.) because it includes all of the eastern North American species,

whereas Hogdon and Steele (1968) dealt only with those of the New England states. It is suspected that the widely varying chromosome numbers reported for some species can be partly attributed to misidentification of the plants. However, that varying chromosome numbers may exist in wild populations is demonstrated by Einset's (1951) comprehensive study of chromosome numbers of offspring following self-pollination, controlled cross-pollinations, and open pollinations of plants with established numbers. An individual polyploid plant ($3x$, $4x$, $5x$, $5x + 1$, $7x$, or $9x$) produced not only apomictic offspring resembling the maternal plant in morphology and chromosome number but also parthenogenetic haploids and true hybrids with varying chromosome numbers as a result of different combinations of reduced and unreduced gametes. The extent to which these deviant chromosome number forms survive and spread in nature depends upon their level of apomixis and/or success of vegetative propagation, their adaptability, and their ability to compete as compared to the species norm from which they were derived.

Chromosome counts have been reported for 45 (22%) of the approximately 200 species of eastern North American blackberries. However, it is clear from Table 1 that the information is scanty, with only a single count for most species, and that there is a very inconsistent pattern in the numbers reported for some species. More cytological information is necessary to determine how much valid intraspecific variation in chromosome number actually does exist. Unfortunately, there have been no significant cytological studies to expand and corroborate the early work of Longley (1924), many of whose plants have suspect identity. The following is an attempt to summarize the limited cytological information for each section.

In section *Alleghenienses*, chromosome counts are $2x$, $3x$, and $4x$. *Rubus allegheniensis* appears to be a well-defined diploid, sexual species. Aalders and Hall's (1966) diploid count for *R. allegheniensis* represented 22 different clones in southwest Nova Scotia. These authors counted chromosomes and studied morphological traits of 470 blackberry plants collected throughout Nova Scotia. They concluded that there were two distinct diploid species, *R. allegheniensis* and *R. hispidus*, and that 355 of the plants studied were triploid hybrids and the remaining 52 were $4x$, $5x$, or $6x$, probably derived from further hybridizations and unreduced gametes. The polyploids all appeared to be facultatively apomictic, which would account for the perpetuation of so many triploid clones. Based on morphological criteria, these triploids were interpreted as having been derived from hybridization of the two basic species, with one of them contributing an unreduced gamete. This study demonstrates the cytotaxonomical complexity facing a botanist attempting to classify the blackberries into discrete species. The two triploid counts for *R. allegheniensis* by Longley (1924) and Einset (1947) most probably were from aberrant plants arising from an unreduced gamete. It is interesting to note that, although *R. allegheniensis* is considered to be a good diploid species, several *allegheniensis*-type tetraploid cultivars (e.g., 'Lawton', 'Ancient Briton', 'Snyder', 'Taylor', and 'Eldorado') have been selected directly from wild populations, although some have been speculated to be interspecific hybrids. In fact, the lineage of the modern eastern upright blackberry cultivars, all tetraploids, traces back to these early wild selections. Obviously, tetraploid forms do appear in nature and, at least some of them, are superior enough in horticultural traits to have been selected for human usage. Because they do not appear to have become a significant part of the population, the question arises about their relative adaptablility in nature as compared to the diploids.

In section *Arguti*, $2x$, $3x$, $4x$, $5x$, $5x + 1$, and $6x$ counts have been reported for various species. I will make no attempt to summarize these because I suspect that the erratic cytological picture reflects misidentified plants in too many cases. It is probable that *R. argutus* is a diploid species, with an occasional triploid aberrant.

The section *Canadenses* is represented here by *R. canadensis*. Craig (1960) reported triploidy in 13 individual clones collected in seven regions of New England, New Brunswick, and Nova Scotia. With three other authors' triploid counts and Einset's (1951) demonstration of apomixis in triploid *R. canadensis*, it appears that this cytotype prevails in a significant part of the range of this species. The three reports of diploid forms indicate that there are also diploid populations.

In section *Cuneifolii*, there are counts of $2x$, $3x$, and $4x$. *Rubus cuneifolius* is a diploid species. Based on meiotic pairing relationships, Spies and DuPlessis (1985) interpreted their individual triploid and tetraploid plants as autopolyploids of the diploid species. These authors made the same conclusion about the triploid and tetraploid *R. pascuus* plants although, in this case, no diploid species was observed.

Section *Flagellares* is the only group in eastern North America in which most species have been consistently reported to be polyploid. I suspect that Longley's (1924) diploid counts for *R. recurvicaulis*

and triploid for *R. biformispinus* and *R. multiformis* were based on misidentified plants. Because many of Longley's (1924) chromosome counts are inconsistent with those of others, the identifications of his plants are highly suspect. The remainder of the counts for this section are 4*x*, 5*x*, 6*x*, 7*x*, 8*x*, and 9*x*, which, if these plants were correctly identified, is strongly suggestive of a polyploid complex similar to that of *R. ursinus* in western North America.

In the section *Hispidi*, 2*x*, 3*x*, 4*x*, 5*x*, and 8*x* counts are reported. Aalders and Hall's (1966) diploid counts for 41 clones of *R. hispidus* collected widely in southwestern Nova Scotia, along with Thompson's (1995a) diploid count from a North Carolina plant, suggest that this is a widespread basic diploid species. It is most likely that Longley's (1924) pentaploid and octoploid counts for *R. hispidus* were mistakenly identified plants, possibly belonging to section *Flagellares*, which has a trailing plant growth habit like the *Hispidi* but, unlike *Hispidi*, is characterized by higher ploidy levels. There is one count each for *R. huttonii* (4*x*), *R. plus* (3*x*), *R. signatus* (3*x*), and *R. tardatus* (3*x*).

In section *Setosi*, chromosome numbers reported are 2*x*, 3*x*, 4*x*, and 5*x*. *Rubus setosus* has both diploid and triploid counts, but with such a limited sampling it is not possible to determine the relative abundance of each of these ploidy levels. There is one count each for *R. dissensus* (3*x*), *R. glandicaulis* (3*x*), *R. clandestinus* (4*x*), *R. hanesii* (4*x*), *R. miscix* (3*x*), *R. notatus* (2*x*), and *R. wisconsinensis* (5*x*).

For section *Triviales*, the only species counted, *R. trivialis*, has been consistently given as diploid by six investigators. There seems to be no question about this being a widespread, basic diploid species.

Although limited cytological information is available for the eastern North American blackberries, a few tentative conclusions are warranted. It appears that, in each section, there is at least one easily recognized species, i.e., the one after which the section is named. Seven of these, *R. alleghaniensis*, *R. argutus*, *R. canadensis*, *R. cuneifolius*, *R. hispidus*, *R. setosus*, and *R. trivialis*, are basically diploid but may have triploid or tetraploid individuals or populations as well. By contrast, the eighth one, *R. flagellaris*, is polyploid, with the predominate chromosome number unknown due to discrepant counts and insufficient sampling. Because of the discrepancies in chromosome numbers, even within species, counts need to be made on population samples rather than individual plants. Such counts made in conjunction with a taxonomic reappraisal would greatly contribute to the clarification of the blackberry species of eastern North America.

The section *Ursini*, represented only by *R. ursinus*, is geographically isolated from all other North American blackberries. It occurs only in the western parts of the Pacific States from southern California to southern British Columbia and in western Idaho. Brown (1943) made an intensive cytotaxonomic study of this species in the southern half of its range and concluded that there were two main chromosome numbers: octoploidy was dominant in most of California, whereas 12*x* was dominant from northern California to southern Oregon, and presumably northward. The limited numbers of plants found with 9*x*, 10*x*, or 11*x*, were assumed to have been derived from the two main chromosome types through hybridization. The relatively few oddploids found suggested that apomixis is not an important mode of reproduction in this species. The lack of consistent morphological traits associated with chromsome number led Brown (1943) to conclude that this western blackberry population consists of only one species with six different ploidy levels.

Subgenus *Rubus* (South American Blackberries)

Of Focke's (1910–1914) four sections of *Rubus* in South and Central America, i.e., *Dissitiflori*, *Xerocarpi*, *Duri*, and *Floribundi*, chromosome counts have been reported for species only in the *Floribundi*. Thus far, the information is very limited, with only one diploid count each for *R. adenotrichos*, *R. robustus*, and *R. urticifolius*, and two for *R. bogotensis*. Should further studies confirm the lack of polyploidy in these blackberries, this cytological situation is a striking contrast to that of this subgenus in North America and Europe.

Proposed Natural Inter-Subgeneric Hybrid

Tetraploid *R. glaucus*, both cultivated and in the wild, is widespread in the northern Andean countries and in Central America. Darrow (1952) first suggested that this species was an allopolyploid originating from hybridization between a black raspberry and a South American blackberry. Jennings's (1978) studies on anthocyanin pigments in *R. glaucus* and its putative parents provided support for this concept.

In conclusion, this compilation provides scientists working with this genus convenient access to the chromosome numbers of species published to date. The current state of knowledge is presented,

and the gaps that need further investigation are made evident. Although counts have been made on an estimated 40 percent of *Rubus* species, many of these are single counts that need confirmation, and the chromosome numbers of the remaining 60 percent of the species need to be determined. It is hoped that this paper will stimulate an interest in additional cytological and taxonomical studies that will contribute to the elucidation of the nature of the species in this large and complex genus.

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Table 1. Chromosome numbers of *Rubus* species. See page 129 for further explanation.

Taxon	2*n*	References
	Subgenus *Chamaemorus* (Hill) Focke	
R. chamaemorus L.	56	Longley 1924; Darrow & Longley 1933; LaCour (Maude 1939); Löve & Löve 1944; Heslop-Harrison 1953; Vaarama 1954; Larsson 1957, 1969; Jørgensen et al. 1958; Sokolovskaya & Strelkova 1960; Löve & Ritchie 1966; Laane 1969; Skalinska et al. 1978; Engelskjon 1979; Löve & Löve 1982a; Zhukova 1982; Krogulevich & Rostovtseva 1984; Dmitrieva & Parfenov 1985
	Subgenus *Chamaebatus* Focke	
R. calycinus Wall. ex D. Don	42	Sharma & Sarkar 1970
R. nivalis Douglas ex Hook.	14	Thompson 1995a
R. pectinellus Maxim.	42	Jinno 1951a, 1958; Iwatsubo & Naruhashi 1993; Thompson & Zhao 1993
	Subgenus *Comaropsis* Focke	
R. geoides Sm.	28	Haskell & Paterson 1966
	Subgenus *Cylactis* Focke	
R. arcticus L.	14	Vaarama 1939; Larsson 1957, 1969; Sokolovskaya & Strelkova 1960; Johnson & Packer 1968; Kotimäki & Hiirsalmi 1979; Belyaeva & Siplivinskiy 1975, 1981; Yurtsev & Zhukova 1982; Thompson 1995a
R. arcticus L.	21	Johnson & Packer 1968; Zhukova 1980
R. arcticus L. subsp. *acaulis* (Michx.) Focke	14	Löve & Löve 1982a
acaulis Michx.	14	Löve & Ritchie 1966
acaulis Michx.	21	Zhukova 1982
Cylactis arcticus (L.) Raf. subsp. *acaulis* (Michx.) W.A. Weber	14	Löve 1987
R. arcticus L. subsp. × *stellarcticus* G. Larsson	14	Thompson 1995a
R. humulifolius C.A. Mey	14	Rostovtseva 1977; Krogulevich & Rostovtseva 1984
R. humulifolius C.A. Mey	28	Vaarama 1939
R. lasiococcus A. Gray	14	Thompson 1995a
R. nepalensis (Hook. f.) Kuntze	28	Gustafsson 1939; Thompson 1995a
R. nutans Wall.	14	Malik 1965
R. nutans Wall.	28	Mehra & Dhawan 1971
R. pedatus Sm.	14	Taylor & Mulligan 1968; Sokolovskaya et al. 1985; Iwatsubo & Naruhashi 1992; Thompson 1995a

Table 1. Continued.

Taxon	2*n*	References
R. pubescens Raf.	14	Löve 1954; Vaarama 1954; Löve & Löve 1966, 1982a, b; Thompson 1995a
Cylactis pubescens (Raf.) W.A. Weber	14	Löve 1987
R. psuedojaponicus Koidz.	14	Iwatsubo & Naruhashi 1993
R. saxatilis L.	28	Scheerer 1939; Vaarama 1939, 1954; Löve & Löve 1944; Löve 1954; Larsson 1957, 1969; Sorsa 1963; Krogulevich 1978; Skalinska et al. 1978; Engelskjon 1979; Löve & Löve 1982b; Dmitrieva & Parfenov 1985
Cylactis saxatilis (L.) Löve	28	Löve 1987
R. stellatus Sm.	14	Vaarama 1954; Larsson 1957, 1969; Kotimäki & Hiirsalmi 1979
R. subarcticus (Greene) Rydb.	14	Longley 1924
Subgenus *Orobatus* Focke		
R. acanthophyllus Focke	42	Thompson 1995a
R. coriaceus Poir.	42	Thompson 1995a
R. glabratus Kunth	42	Thompson 1995a
R. macrocarpus Benth.	42	Dale & Ingram 1981
R. nubigenus Kunth	42	Thompson 1995a
R. roseus Poir.	42	Thompson 1995a
Subgenus *Dalibardastrum* (Focke) Yü & Lu		
R. amphidasys Focke ex Diels	42	Thompson & Zhao 1993
R. tricolor Focke	28	Keep 1958; Iwatsubo & Naruhashi 1993; Thompson & Zhao 1993
R. tsangorum Hand.-Mazz.	28	Thompson 1995a
Subgenus *Malachobatus* Focke		
R. acuminatus Sm.	28	Malla et al. 1975; Iwatsubo & Naruhashi 1992
R. assamensis Focke	28	Thompson & Zhao 1993
R. bambusarum Focke	28	Thompson & Zhao 1993
R. henryi Hemsl. & Kuntze var. *bambusarum* (Focke) Rehder	28	Keep 1958
R. buergeri Miq.	42	Naruhashi & Iwatsubo 1993
R. buergeri Miq.	56	Jinno 1951a, 1958; Britton & Hull 1957; Iwatsubo et al. 1992; Naruhashi & Iwatsubo 1993; Thompson & Zhao 1993
R. caudifolius Wuzhi	28	Thompson & Zhao 1993
R. chroosepalus Focke	28	Thompson & Zhao 1993

Table 1. Continued.

Taxon	2*n*	References
R. crassifolius Yü & Lu	28	Thompson & Zhao 1993
R. dolichophyllus Hand.-Mazz.	28	Thompson & Zhao 1993
R. echinoides Metc.	28	Thompson & Zhao 1993
R. fairholmianus Gardner	14	Subramanian 1987
R. fairholmianus Gardner	56	Nybom 1986
R. feddei Lév. & Vaniot	28	Thompson & Zhao 1993
R. formosensis Kuntze	28	Thompson & Zhao 1993
R. fulvus Focke	14	Subramanian 1987
R. gardnerianus Kuntze	14	Subramanian 1987
R. gardnerianus Kuntze	56	Gill et al. 1984; Singhal et al. 1990
R. glomeratus Blume	98	Borgmann 1964 (No. 200)
R. hakonensis Franch. & Sav.	42	Jinno 1958; Naruhashi & Iwatsubo 1993
R. hakonensis Franch. & Sav.	56	Jinno 1951b, 1958; Naruhashi & Iwatsubo 1993
R. hayata-koidzumii Naruh.	28	Iwatsubo & Naruhashi 1993; Thompson & Zhao 1993
R. calycinoides Hayata var. *macrophyllus* Li	14	Hsu 1968
R. henryi Hemsl. & Kuntze	28	Thompson 1995a
R. hexagynus Roxb.	28	Sarkar et al. 1977
R. hillii F. Muell.	42	Thompson 1995a
R. hunanensis Hand.-Mazz.	28	Thompson 1995a
R. ichangensis Hemsl. & Kuntze	28	Iwatsubo & Naruhashi 1992; Thompson & Zhao 1993
R. indicus Thunb.	56	Nybom 1980, 1986
R. irenaeus Focke	42	Thompson & Zhao 1993
R. lambertianus Ser.	28	Iwatsubo & Naruhashi 1992; Thompson & Zhao 1993
R. lambertianus Ser. var. *glaber* Hemsl.	28	Thompson 1995a
R. lambertianus Ser. var. *glandulosus* Card.		
R. morii Hayata	28	Hsu 1968
R. mallotifolius Wu ex Yü & Lu	28	Thompson & Zhao 1993
R. micropetalus Gardner	14	Subramanian 1987
R. moluccanus L.	28	Nybom 1986
R. multibracteatus Lév. & Vaniot	28	Thompson & Zhao 1993
R. nesiotes Focke	28	Iwatsubo & Naruhashi 1993
R. paniculatus Sm.	14	Malik 1965; Mehra & Dhawan 1966
R. reflexus Ker	42	Thompson & Zhao 1993
R. rugosus Sm.	14	Malla et al. 1975; Subramanian 1987
R. rugosus Sm.	56	Iwatsubo & Naruhashi 1992
R. rugosus Sm.	98	Nybom 1986

Table 1. Continued.

Taxon	2*n*	References
R. rugosus Sm. var. *thwaitesii* Focke	98	Nybom 1980
R. rugosus Sm. cv. Keriberry	98	Thompson 1995b
R. setchuenensis Bureau & Franch.	28	Iwatsubo & Naruhashi 1993; Thompson & Zhao 1993
R. omeiensis Rolfe	28	Marks 1952
R. sieboldii Blume	28	Jinno 1951a, 1958; Iwatsubo et al. 1992; Iwatsubo & Naruhashi 1992
R. swinhoei Hance	28	Thompson 1995a
R. tephrodes Hance	28	Vaarama 1954; Thompson & Zhao 1993
R. tephrodes Hance var. *ampliflorus* (Lév. & Vaniot) Hand.-Mazz.	28	Thompson 1995a
R. tiliaceus Sm.	28	Iwatsubo & Naruhashi 1993
R. tsangorum Hand.-Mazz.	28	Thompson 1995a
R. xanthoneurus Focke ex Diels	28	Thompson & Zhao 1993
Subgenus *Anoplobatus* Focke		
R. deliciosus Torr.	14	Thompson 1995a
R. deliciosus Torr.	21	Longley 1924
R. neomexicanus A. Gray	14	Thompson 1995a
R. odoratus L.	14	Longley 1924; Yeager & Meader 1958; Wcislo 1987; Thompson 1995a
Rubacer odoratum (L.) Rydb.	14	Löve 1987
R. parviflorus Nutt.	14	Darrow & Longley 1933; Vaarama 1954; Taylor & Mulligan 1968; Thompson 1995a
Rubacer parviflorum (Nutt.) Rydb.	14	Löve 1987
Subgenus *Idaeobatus* Focke		
R. adenophorus Rolfe	14	Longley & Darrow 1924; Thompson & Zhao 1993
R. apetalus Poir.	14	Spies & DuPlessis 1985; Spies et al. 1985
R. apetalus Poir.	28	Spies & DuPlessis 1985; Spies et al. 1985
R. archboldianus Merr. & Perry	ca. 91	Borgmann 1964 (No. 65)
R. biflorus Buch.-Ham. ex Smith	14	Williams et al. 1949; Malik 1965; Mehra & Dhawan 1966
R. chingii Hu	14	Iwatsubo & Naruhashi 1992; Thompson & Zhao 1993
R. cockburnianus Hemsl.	14	Thompson & Zhao 1993; Thompson 1995a
R. giraldianus Focke ex Diels	14	Vaarama 1954; Britton & Hull 1957
R. columellaris Tutcher	14	Thompson & Zhao 1993; Thompson 1995a
R. commersonii Poir.	14	Iwatsubo & Naruhashi 1993
R. corchorifolius L.f.	14	Iwatsubo & Naruhashi 1993; Thompson & Zhao 1993; Thompson 1995a

Table 1. Continued.

Taxon	2*n*	References
R. coreanus Miq.	14	Longley & Darrow 1924; Williams et al. 1949; Marks 1952; Britton & Hull 1957; Pool et al. 1981; Iwatsubo & Naruhashi 1991; Thompson & Zhao 1993; Thompson 1995a
R. crataegifolius Bunge	14	Vaarama 1954; Keep 1958; Naruhashi 1989; Iwatsubo & Naruhashi 1992; Thompson & Zhao 1993; Thompson 1995a
R. wrightii A. Gray	14	Jinno 1951b, 1958
R. croceacanthus Lév.	14	Iwatsubo & Naruhashi 1992
R. ellipticus Sm.	14	Malik 1965; Mehra & Dhawan 1966; Mehra et al. 1973; Malla et al. 1974; Gill et al. 1984; Subramanian 1987; Singhal et al. 1990; Iwatsubo & Naruhashi 1992; Thompson & Zhao 1993; Thompson 1995a
R. eustephanos Focke ex Diels	14	Thompson 1995a
R. flosculosus Focke	14	Vaarama 1954; Britton & Hull 1957; Thompson & Zhao 1993; Thompson 1995a
R. foliolosus D. Don	14	Malik 1965; Iwatsubo & Naruhashi 1993
R. foliolosus D. Don	28	Malla et al. 1977
R. grayanus Maxim.	14	Iwatsubo & Naruhashi 1993
R. hawaiensis A. Gray	14	Keep 1958; Thompson 1995a
R. hirsutus Thunb.	14	Jinno 1951a, 1958; Naruhashi 1989; Iwatsubo & Naruhashi 1992; Thompson & Zhao 1993; Thompson 1995a
R. hoffmeisterianus Kunth & Bouche	14	Thompson 1995a
R. hypargyrus Edgew. var. *niveus* H. Hara		
R. gracilis Roxb. sensu Focke	14	Marks 1952; Britton & Hull 1957
R. niveus Wall. ex G. Don	14	Malik 1965; Britton & Hull 1957
R. niveus Wall. ex G. Don	28	Mehra et al. 1973
R. pedunculosus D. Don sensu Wall.	14	Britton & Hull 1957
R. idaeopsis Focke	14	Thompson & Zhao 1993
R. idaeus L.	14	Longley & Darrow 1924; Crane & Darlington 1927; Yarnell 1932; Rozanova 1934, 1940; Rohweder 1937; Thomas 1940b; Heslop-Harrison 1953; Einset & Pratt 1954; Larsson 1969; Skalinska et al. 1978; Engelskjon 1979; Pool et al. 1981; Dmitrieva & Parfenov 1985; Thompson 1995a
R. idaeus L. var. *anomalus* Arrh.	14	Vaarama 1939
R. idaeus L. var. *buschii* Rozanova		
R. buschii (Rozanova) Grossh. ex Sinkova	14	Magulaev 1976
R. ikenoensis Lév. & Vaniot	14	Iwatsubo & Naruhashi 1992; Thompson 1995a

Table 1. Continued.

Taxon	2*n*	References
R. japonicus Maxim.	14	Jinno 1958
R. illecebrosus Focke	14	Longley 1924; Longley & Darrow 1924; Jinno 1951b, 1958; Thompson 1995a
R. innominatus S. Moore	14	Longley & Darrow 1924; Britton & Hull 1957; Iwatsubo & Naruhashi 1993; Thompson & Zhao 1993; Thompson 1995a
R. innominatus S. Moore var. *kuntzeanus* (Hemsl.) L.H. Bailey		
R. kuntzeanus Hemsl.	14	Williams et al. 1949
R. inopertus (Diels) Focke	14	Vaarama 1954; Britton & Hull 1957; Thompson & Zhao 1993
R. kisoensis Nakai	14	Naruhashi 1972
R. lasiostylus Focke	14	Longley & Darrow 1924; Britton & Hull 1957; Thompson & Zhao 1993; Thompson 1995a
R. lasiostylus Focke var. *hubeiensis* T.T. Yü et al.	14	Thompson 1995a
R. leucocarpus Arn.	28	Iwatsubo & Naruhashi 1993
R. leucodermis Douglas ex Torrey & A. Gray	14	Darrow & Longley 1933; Thompson 1995a
R. longipedicellatus (Gust.) C.H. Stirt.	14	Spies & DuPlessis 1985; Spies et al. 1985
R. longipedicellatus (Gust.) C.H. Stirt.	28	Spies & DuPlessis 1985; Spies et al. 1985
R. longipedicellatus (Gust.) C.H. Stirt	35	Spies & DuPlessis 1985; Spies et al. 1985
R. lorentzianus Pulle	126	Borgmann 1964 (No. 48)
R. ludwigii Eckl. & Zeyh.	14	Britton & Hull 1957; Spies & DuPlessis 1985; Spies et al. 1985
R. macilentus Cambess.	14	Malik 1965
R. mcvaughnianus Rzed. & Calderon	14	Thompson 1995a
R. mesogaeus Focke	14	Longley & Darrow 1924; Jinno 1958
R. microphyllus L.f.	14	Iwatsubo & Naruhashi 1992
R. microphyllus L.f. var. *incisus* Koidz.	14	Jinno 1958
R. minusculus Lév. & Vaniot	14	Iwatsubo & Naruhashi 1993; Thompson 1995a
R. montis-wilhelmii P. Royen	14	Borgmann 1964
R. nishimuranus Koidz.	28	Ono 1977; Iwatsubo & Naruhashi 1992
R. niveus Thunb.	14	Thomas 1940b; Britton & Hull 1957; Malik 1965; Mehra & Dhawan 1966; Subramanian 1987; Iwatsubo & Naruhashi 1993; Thompson & Zhao 1993; Thompson 1995a
R. albescens Roxb.	14	Britton & Hull 1957
R. lasiocarpus Sm.	14	Vaarama 1954; Malik 1965; Mehra & Dhawan 1966
R. niveus Thunb.	28	Mehra et al. 1973
R. occidentalis L.	14	Longley 1924; Longley & Darrow 1924; Thompson 1995a
R. okinawensis Koidz.	14	Iwatsubo & Naruhashi 1993

Table 1. Continued.

Taxon	2*n*	References
R. palmatus Thunb. ex Murray	14	Iwatsubo & Naruhashi 1992; Thompson 1995a
R. coptophyllus A. Gray	14	Jinno 1958
R. fauriei Lév. & Vaniot	14	Jinno 1951b, 1958
R. palmatoides Kuntze	14	Jinno 1951b, 1958
R. palmatus Thunb. ex Murray var. *coptophyllus* (A. Gray) Kuntze	14	Thompson 1995a
R. parvifolius L.	14	Jinno 1951a, 1958; Williams et al. 1949; Britton & Hull 1957; Bammi 1965b; Probatova et al. 1989; Iwatsubo & Naruhashi 1991; Thompson & Zhao 1993; Thompson 1995a
R. triphyllus Thunb.	14	Longley 1924
R. parvifolius L.	21	Naruhashi & Iwatsubo 1993
R. peltatus Maxim.	14	Jinno 1958; Iwatsubo & Naruhashi 1992
R. phoenicolasius Maxim.	14	Longley & Darrow 1924; Chomisury 1927; Jinno 1951b, 1958; Britton & Hull 1957; Iwatsubo & Naruhashi 1993; Thompson & Zhao 1993
R. pinfaensis Lév. & Vaniot	14	Thompson 1995a
R. pinnatus Willd.	14	Spies & DuPlessis 1985; Spies et al. 1985
R. pinnatus Willd.	28	Spies & DuPlessis 1985; Spies et al. 1985
R. probus L.H. Bailey		
R. muelleri F.M. Bailey	28	Thompson 1995a
R. pseudoacer Makino	14	Jinno 1958; Iwatsubo & Naruhashi 1993
R. pungens Cambess.	14	Iwatsubo & Naruhashi 1992; Thompson & Zhao 1993; Thompson 1995a
R. racemosus Roxb.	14	Subramanian 1987
R. ribisoideus Matsum.	14	Jinno 1958
R. rosifolius Sm.	14	Thompson & Zhao 1993; Thompson 1995a
R. rosifolius Sm. var. *coronarius* (Sims.) Focke	14	Thompson 1995a
R. sachalinensis Lév.	28	Rozanova 1939; Krogulevich 1976, 1978; Krogulevich & Rostovtseva 1984; Zhukova et al. 1977; Yurtsev & Zhukova 1982; Thompson 1995a
R. idaeus L. var. *melanolasius* Focke (N.E. Asia)	28	Rozanova 1939
R. idaeus L. var. *sachalinensis* (Lév.) Focke (N.E. Asia)	28	Rozanova 1939
R. idaeus L. var. *sibiricus* Kom. (N.E. Asia)	28	Rozanova 1939
R. simplex Focke	14	Vaarama 1954; Iwatsubo & Naruhashi 1993; Thompson & Zhao 1993; Thompson 1995a
R. spectabilis Pursh.	14	Darrow & Longley 1933; Taylor & Mulligan 1968; Iwatsubo & Naruhashi 1992; Thompson 1995a

Table 1. Continued.

Taxon	2*n*	References
R. strigosus Michx.	14	Longley & Darrow 1924; Yarnell 1936; Rozanova 1939; Fischer et al. 1941; Williams et al. 1949; Einset & Pratt 1954; Vaarama 1954; Thompson 1995a
R. idaeus L. var. *canadensis* Richardson	14	Longley 1924
R. idaeus L. var. *melanolasius* Focke (No. Amer.)	14	Löve & Löve 1982a; Packer & Witkus 1982
R. idaeus L. var. *sachalinenesis* (Lev.) Focke (No. Amer.)	14	Löve & Löve 1966
R. idaeus L. var. *strigosus* Michx.	14	Yarnell 1932; Einset & Pratt 1954
R. strigosus Michx.	21	Einset 1947
R. subcrataegifolius (Lév. & Vaniot) Lév. & Vaniot		
R. koehneanus Focke	14	Jinno 1958
R. microphyllus L.f. var. *subcrataegifolius* Lév. & Vaniot	14	Thompson 1995a
R. sumatranus Miq.	14	Iwatsubo & Naruhashi 1992; Thompson & Zhao 1993; Thompson 1995a
R. asper Wall. ex D. Don	14	Jinno 1958
R. thibetanus Franch.	14	Britton & Hull 1957; Thompson & Zhao 1993
R. tokin-ibara Naruh.		
R. commersonii auct. Japon., non Poir	14	Jinno 1951b, 1958
R. eustephanos Focke var. *coronarius* Koidz.	14	Jinno 1958
R. trianthus Focke	14	Thompson & Zhao 1993; Thompson 1995a
R. trifidus Thunb. ex Murray	14	Jinno 1951b, 1958; Iwatsubo & Naruhashi 1992; Thompson 1995a
R. vernus Focke	14	Iwatsubo & Naruhashi 1993
R. xanthocarpus Bureau & Franch.	14	Gustafsson 1933
R. yabei Lév. & Vaniot	14	Jinno 1958
R. yoshinoi Koidz.	14	Naruhashi & Iwatsubo 1993
R. yoshinoi Koidz.	21	Naruhashi & Iwatsubo 1993
Subgenus *Micranthobatus* (Fritsch) Kalkman (= *Lampobatus* sensu Focke pro parte)		
R. cissoides A. Cunn.	28	Thompson 1995a
R. parvus Buchanan	28	Beuzenberg & Hair 1983
R. royenii Kalkman var. *hispidus* Kalkman	28	Borgmann 1964 (No. 203)
R. schmidelioides A. Cunn.	28	Thompson 1995a
R. squarrosus Fritsch	28	Thompson 1995a

Table 1. Continued.

Taxon	2*n*	References
Subgenus *Rubus* L. (European blackberry species)		
Section *Rubus*		
R. adscitus Genev. subsp. *macrothyrsus* Lange	28	Beijerinck 1956
R. adornatus P.J. Müll.	28	Beijerinck 1956
R. adspersus Weihe ex H.E. Weber	28	Iwatsubo et al. 1995
R. ahenifolius W.C.R. Watson	28	Heslop-Harrison 1953
R. amisiensis H.E. Weber	28	Iwatsubo et al. 1995
R. amplificatus Lees	28	Heslop-Harrison 1953
R. schlechtendalii auct. pro parte, non Weihe ex Link	28	Crane 1935; Fabergé (Maude 1939)
R. anglocandicans A. Newton		
R. falcatus auct.	35	Heslop-Harrison 1953
(as *R. thyrsoideus* sp. coll.)	35	Marks 1952
R. apricus Wimm.	28	Boratynska 1995
R. armeniacus Focke	28	Gustafsson 1943; Thompson 1995a
(as *R. procerus* P.J. Müll. cv. Himalaya)	28	Darrow & Longley 1933; Crane 1935; Berger 1953; Beijerinck 1956; Markarian & Olmo 1959; Haskell 1960; Haskell & Tun 1961; Bammi 1965a; Bammi & Olmo 1966
R. armipotens W.C. Barton ex A. Newton		
R. pseudobifrons (sensu W.C.R. Watson, non Sudre)	28	Harrison (Maude 1939); Heslop-Harrison 1953
R. arrhenii (Lange) Lange	28	Gustafsson 1933, 1939; Beijerinck 1956
R. arrhenii (Lange) Lange var.	28	Heslop-Harrison 1953
R. atrichantherus E.H.L. Krause grex *mucronatus*	28	Gustafsson 1939
R. axillaris Lej.	28	Thompson 1995a
R. scanicus Aresch.	28	Harrison (Maude 1939); Gustafsson 1939, 1943
R. badius Focke	28	Beijerinck 1956
R. bakerianus W.C. Barton & Ridd.	28	Heslop-Harrison 1953
R. bartonii A. Newton cv. Ashton Cross	28	Thompson 1995b
R. bertramii G. Braun	28	Harrison (Maude 1939)
R. bifrons Vest	28	Christen 1950
R. bloxamianus Colemanex Purchas	42	Harrison (Maude 1939)
R. bloxamii (Bab.) Lees	28	Datta 1932
R. boraeanus Genev.	28	Heslop-Harrison 1953
R. bregutiensis A. Kern. ex Focke	28	Christen 1950
R. brevistaminosus Edees & A. Newton		
(as *R. braeuckeri* sensu W.C.R. Watson (1958), non G. Braun)	21	Heslop-Harrison 1953
R. calvatus Lees ex A. Bloxam	28	Haskell 1960

Table 1. Continued.

Taxon	2*n*	References
R. canescens DC.	14	Gilli 1969; Thompson 1995a
R. tomentosus Borkh. pro parte	14	Gustafsson 1933, 1939, 1943; Christen 1950; Berger 1953; Beijerinck 1956; Haskell 1960; Haskell & Tun 1961
R. tomentosus Borkh. var. *glabratus* Godr.	14	Markova 1968
R. cardiophyllus Lefèvre & P. J. Müll.	28	Harrison (Maude 1939); Heslop-Harrison 1953
R. caucasicus Focke	28	Thompson 1995a
R. chaerophyllus Sagorski & W. Schultze var. *chaerophyllus*	28	Beijerinck 1956
R. chloophyllus Sudre (as *R. bertramii* G. Braun)	28	Harrison (Maude 1939)
R. chlorothyrsus Focke	28	Beijerinck 1956
R. chrysoxylon (W.M. Rogers) W.M. Rogers	28	Harrison (Maude 1939)
R. cimbricus Focke	28	Gustafsson 1939
R. cissburiensis W.C. Barton & Ridd. (as *R. separinus* Genev.)	28	Heslop-Harrison 1953
(as *R. separinus* Genev., dwarf form)	28	Heslop-Harrison 1953
R. clusii Borbas		
R. gremlii Focke	28	Gilli 1969
R. conothyrsoides H.E. Weber	28	Iwatsubo et al. 1995; Thompson 1995a
R. crespignyanus W.C.R. Watson (as *R. calvatus* Lees)	28	Heslop-Harrison 1953
R. cyri Juz.	28	Crane 1935
R. dasyphyllus (W.M. Rogers) E.S. Marshall	28	Thompson 1995a
R. dentatifolius (Briggs) W.C.R. Watson (as *R. uncinatus* P.J. Müll.)	28	Gustafsson 1939, 1943; Iwatsubo et al. 1995
R. distractus P. J. Müll. ex. Wirtg.	28	Harrison (Maude 1939)
R. menkei Weihe	28	Beijerinck 1956
R. divaricatus P.J. Müll.		
R. nitidus auct., non Weihe & Nees	21	Heslop-Harrison 1953
R. nitidus auct., non Weihe & Nees	28	Datta 1932
R. nitidus Weihe & Nees pro parte	21	Gustafsson 1943; Beijerinck 1956
R. diversus W.C.R. Watson	28	Heslop-Harrison 1953
R. drejeri Jensen ex Lange	28	Gustafsson 1939; Thompson 1995a
R. drejeri Jensen ex Lange	35	Marks 1952
R. dumnoniensis Bab.	28	Harrison (Maude 1939); Heslop-Harrison 1953
R. echinatoides (W.M. Rogers) Dallman	28	Heslop-Harrison 1953
R. echinatus Lindl.		

Table 1. Continued.

Taxon	2*n*	References
R. discerptus P.J. Müll	28	Harrison (Maude 1939)
R. egregius Focke	28	Gustafsson 1939; Heslop-Harrison 1953; Beijerinck 1956
R. elatior Focke ex Gremli	21	Gustafsson 1943
R. elegantispinosus (A. Schumach.) H.E. Weber	28	Iwatsubo et al. 1995
R. errabundus W.C.R. Watson	28	Heslop-Harrison 1953
R. erythrops Edees & A. Newton	28	Thompson 1995a
R. rosaceus sensu W.C.R. Watson, non Weihe	28	Faberge (Maude 1939); Heslop-Harrison 1953
R. fissus Lindl.	21	Beijerinck 1956
R. fissus Lindl.	28	Gustafsson 1939; Heslop-Harrison 1953
R. foliosus Weihe	28	Iwatsubo et al. 1995
R. foliosus Weihe subsp. *flexuosus* P.J. Müll.	28	Beijerinck 1956
R. formidabilis Lefèvre & P.J. Müll.	28	Harrison (Maude 1939)
R. formidabilis Lefèvre & P.J. Müll.	35	Heslop-Harrison 1953
R. furvicolor Focke	28	Heslop-Harrison 1953
(as *R. leyanus* W.M. Rogers)	28	Harrison (Maude 1939)
R. gelertii Frid.	28	Gustafsson 1939; Iwatsubo et al. 1995
R. geniculatus Kaltenb.	28	Beijerinck 1956
R. georgicus Focke	28	Thompson 1995a
R. glandithyrsos G. Braun	28	Iwatsubo et al. 1995
R. glanduliger W.C.R. Watson	28	Heslop-Harrison 1953
R. glandulosus Bellardi	28	Thompson 1995a
R. gliviciensis Sprib.	28	Boratynska 1994
R. godronii Lecoq & Lamotte subsp. *winteri* P.J. Müll.	28	Beijerinck 1956
R. grabowskii Weihe ex Gunther et al.		
R. thyrsanthus Focke	21	Gustafsson 1939, 1943
R. thyrsanthus Focke var. *subvelutinus* Lindeb.		
R. subvelutinus Ripart	21	Gustafsson 1939
R. thyrsoideus Wimm. agg.	21	Longley 1924; Christen 1950
R. gracilis J. & C. Presl	28	Boratynska 1994
R. villicaulis Köhler	28	Beijerinck 1956
R. gratus Focke	28	Fabergé (Maude 1939); Heslop-Harrison 1953; Beijerinck 1956
R. griffithianus W.M. Rogers	28	Heslop-Harrison 1953
R. hartmanii Gand.	28	Thompson 1995a
R. horridus Hartm.	28	Gustafsson 1943
R. hartmanii Gand.	35	Heslop-Harrison 1953

Table 1. Continued.

Taxon	2*n*	References
R. hastiformis W.C.R. Watson		
R. thyrsiger Bab.	28	Crane & Darlington 1927; Crane 1935; Thomas 1940a
R. heterobelus Sudre	28	Harrison (Maude 1939); Heslop-Harrison 1953
R. hylophilus Ripley ex Genev.		
R. brittonii W.C. Barton & Ridd.	21	Heslop-Harrison 1953
R. hypomalacus Focke	28	Beijerinck 1956; Iwatsubo et al. 1995
R. imbricatus Hort	28	Datta 1932; Heslop-Harrison 1953
R. incurvatus Bab.	28	Datta 1932; Heslop-Harrison 1953
R. infestisepalus Edees & A. Newton		
R. macrothyrsus sensu W.C.R. Watson (1958), non Lange	14	Harrison (Maude 1939)
R. macrothyrsus sensu W.C.R. Watson (1958), non Lange	28	Harrison (Maude 1939); Heslop-Harrison 1953
R. macrothyrsus sensu W.C.R. Watson (1958), non Lange (dwarf form)	28	Heslop-Harrison 1953
R. infestus Weihe ex Boenn.	28	Fabergé (Maude 1939); Heslop-Harrison 1953
R. infestus Weihe ex Boenn.	42	Fabergé (Maude 1939)
R. taenarium Lindeb.	28	Gustafsson 1939
R. insularis F. Aresch.	28	Gustafsson 1933, 1939, 1943; Thompson 1995a
R. insularis Aresch. subsp. *confinus* (LDGB.) F. Aresch.		
R. confinus Lindeb.	28	Gustafsson 1939
R. iricus Rogers		
(as *R. insularis* F. Aresch.)	28	Harrison (Maude 1939)
R. kollundicola Gust.	35	Gustafsson 1939
R. laciniatus Willd.	28	Crane & Darlington 1927; Crane 1935; Heslop-Harrison 1953; Haskell 1960; Bammi 1965a; Bammi & Olmo 1966; Thompson 1995a
R. langei Jensen ex K. Frid. & Gelert	28	Gustafsson 1939
R. largificus W.C.R. Watson	28	Harrison (Maude 1939); Heslop-Harrison 1953
R. lentiginosus Lees	28	Fabergé (Maude 39)
R. lentiginosus Lees	35	Marks 1952
R. lespinassei Clavaud		
R. coutinhi Samp.	28	Marks 1952
R. leucandriformis Edees & A. Newton		
R. leucandrus sensu W.C.R. Watson (1958), non Focke	28	Heslop-Harrison 1953
R. leucandrus Focke	28	Iwatsubo et al. 1995
R. leucostachys Schleich. ex Sm.		
R. leucostachys Sm.	28	Heslop-Harrison 1953
(as *R. lasioclados* Focke var. *angustifolius* W.M. Rogers)	21	Heslop-Harrison 1953

Table 1. Continued.

Taxon	2*n*	References
R. lindebergii P.J. Müll.	28	Gustafsson 1939; Heslop-Harrison 1953; Iwatsubo et al. 1995
R. lindleyanus Lees	28	Datta 1932; Beijerinck 1956
R. longifrons W.C.R. Watson		
R. longifolius W.C.R. Watson	28	Harrison (Maude 1939)
R. macrophyllus Weihe & Nees	28	Gustafsson 1943; Heslop-Harrison 1953; Beijerinck 1956; Boratynska 1995; Iwatsubo et al. 1995
R. macrophyllus Weihe & Nees var. *megaphyllus* (P.J. Müll.) Sudre	28	Gustafsson 1943
R. marshallii Focke & W.M. Rogers	35	Heslop-Harrison 1953
R. melanodermis Focke	28	Faberge (Maude 1939)
R. mercicus Bagn.	28	Heslop-Harrison 1953
R. milesii A. Newton		
R. spinulifer auct.	28	Heslop-Harrison 1953
R. koehleri auct.	28	Harrison (Maude 1939)
R. koehleri auct.	35	Marks 1952
R. miszczenkoi Juz.	28	Thompson 1995a
R. mollissimus W.M. Rogers	28	Harrison (Maude 1939)
R. montanus Lib. ex Lej.	21	Iwatsubo et al. 1995
R. candicans Weihe ex Rchb.	21	Gustafsson 1939, 1943; Gilli 1969
R. mucronulatus Boreau		
R. mucronatus Bloxam	28	Beijerinck 1956
R. muenteri T. Marsson	28	Iwatsubo et al. 1995
R. scheutzii Lindeb.	28	Gustafsson 1939, 1943
R. murrayi Sudre	28	Heslop-Harrison 1953
R. adornatus auct.	28	Heslop-Harrison 1953
R. naldretti (J.W. White) W.C.R. Watson	28	Heslop-Harrison 1953
R. nemoralis P.J. Müll.	28	Heslop-Harrison 1953; Boratynska 1994
R. selmeri Lindeb.	28	Fabergé (Maude 1939); Gustafsson 1939
R. nemoralis P.J. Müll. var. *microphyllus* (Lindeb.) W.C.R. Watson	28	Heslop-Harrison 1953
R. neomalacus Sudre	28	Heslop-Harrison 1953
R. nessensis Hall	28	Gustafsson 1943; Heslop-Harrison 1953; Beijerinck 1956; Dmitrieva & Parfenov 1985; Boratynska 1995
R. suberectus G. Anderson	28	Gustafsson 1933, 1939; Christen 1950
R. newbouldii Bab.	28	Harrison (Maude 1939)
R. newbridgensis W.C. Barton & Ridd.	28	Heslop-Harrison 1953
R. newbridgensis W.C. Barton & Ridd.	42	Heslop-Harrison 1953

Table 1. Continued.

Taxon	2*n*	References
R. nitidiformis Sudre		
R. nitidoides W.C.R. Watson	28	Crane 1935; Fabergé (Maude 1939); Thomas 1940a; Heslop-Harrison 1953; Haskell 1960
R. nitidoides W.C.R. Watson	42	Harrison (Maude 1939)
R. oxyanchus Sudre	28	Heslop-Harrison 1953
R. pallidus Weihe	28	Gustafsson 1933, 1939; Heslop-Harrison 1953; Beijerinck 1956
R. patuliformis Sudre	28	Heslop-Harrison 1953
R. pedemontanus Pinkw.	35	Boratynska 1995; Iwatsubo et al. 1995
R. bellardii Weihe & Nees	35	Gustafsson 1933, 1939; Beijerinck 1956
R. bellardii Weihe & Nees	28	Fabergé (Maude 1939)
R. bellardii Weihe	28	Heslop-Harrison 1953; Czapik 1987
R. permundus W.C.R. Watson (as *R. axillaris* P.J. Müll.)	28	Harrison (Maude 1939)
R. phaeocarpus W.C.R. Watson	28	Heslop-Harrison 1953
R. platyacanthus P.J. Müll. & Lefèvre	28	Iwatsubo et al. 1995
R. carpinifolius Weihe	28	Beijerinck 1956
R. carpinifolius auct.	35	Marks 1952
R. plicatus Weihe & Nees	28	Gustafsson 1933, 1939, 1943; Heslop-Harrison 1953; Vaarama 1951; Beijerinck 1956; Boratynska 1995; Thompson 1995a
R. polyanthemus Lindeb.	28	Gustafsson 1933, 1939, 1943; Heslop-Harrison 1953; Beijerinck 1956; Iwatsubo et al. 1995
R. polyanthemus Lindeb. (dwarf form)	28	Heslop-Harrison 1953
R. praecox Bertoloni	28	Iwatsubo et al. 1995
R. prolongatus Boulay & Letendre ex Corb. (as *R. chrysoxylon* W.M. Rogers)	28	Harrison (Maude 1939)
R. pseudopallidus Gust. ex A. Gust. *R. pallidus* Weihe f. *suecius*	28	Gustafsson 1933, 1939
R. pyramidaliformis (Sudre) Ziel.	28	Boratynska 1994
R. pyramidalis Kaltenb.	26–28	Gustafsson 1943
R. pyramidalis Kaltenb.	28	Heslop-Harrison 1953; Beijerinck 1956; Haskell & Tun 1961; Thompson 1995a
R. pyramidalis Kaltenb. var. *parvifolius* Frid. & Gelert	28	Heslop-Harrison 1953
R. pyramidalis Kaltenb. var. *parvifolius* Frid. & Gelert	42	Heslop-Harrison 1953
R. questieri Lefèvre & P.J. Müll.	28	Harrison (Maude 1939)

Table 1. Continued.

Taxon	2*n*	References
R. radula Weihe ex Boenn.	28	Fabergé (Maude 1939); Gustafsson 1933, 1939; Heslop-Harrison 1953; Markova 1972; Boratynska 1994
R. radula Weihe ex Boenn. var. *angustifolius* Lund	28	Gustafsson 1933, 1939
R. radula Weihe ex Boenn. var. *microphyllus* Lindeb.	28	Heslop-Harrison 1953
R. rhombifolius Weihe ex Boenn.	28	Fabergé (Maude 1939); Iwatsubo et al. 1995
R. rosaceus Weihe	28	Beijerinck 1956
R. rotundifolius (Bab.) A. Bloxam	28	Harrison (Maude 1939); Heslop-Harrison 1953
R. rubritinctus W.C.R. Watson		
R. cryptadenes Sudre	28	Fabergé (Maude 1939); Heslop-Harrison 1953
R. rudis Weihe	28	Gustafsson 1939; Berger 1953; Beijerinck 1956
R. rufescens Lefèvre & P.J. Müll.	28	Heslop-Harrison 1953
R. salteri Bab.	28	Fabergé (Maude 1939)
R. sanctus Schreb.	14	Thompson 1995a
R. sanguineus Friv.	14	Markova 1968
R. scaber Weihe	28	Fabergé (Maude 1939); Heslop-Harrison 1953
R. schlechtendalii Weihe	28	Beijerinck 1956
R. schleicheri Weihe ex Tratt. subsp. *schleicheri*	28	Beijerinck 1956
R. schnedleri H.E. Weber	28	Boratynska 1994
R. scidularum A. Beek	28	Beek 1981
R. sciocharis (Sudre) W.C.R. Watson	28	Heslop-Harrison 1953
R. sciaphilus Lange	28	Gustafsson 1939, 1943
R. scissus W.C.R. Watson f. *acicularis* F. Aresch.	28	Heslop-Harrison 1953
R. senticosus Kohler ex Weihe	28	Beijerinck 1956; Iwatsubo et al. 1995
R. montanus Wirtg.	28	Gustafsson 1943
R. septentrionalis W.C.R. Watson		
R. confinis Lindeb.	28	Gustafsson 1939
R. silvaticus Weihe & Nees	28	Heslop-Harrison 1953; Beijerinck 1956; Iwatsubo et al. 1995
R. sprengelii Weihe	28	Datta 1932; Gustafsson 1933, 1939; Harrison (Maude 1939); Heslop-Harrison 1953; Beijerinck 1956
R. subinermoides Druce	28	Heslop-Harrison 1953
R. sulcatus Vest	28	Fabergé (Maude 1939); Gilli 1969
R. sulcatus Vest	±28	Gustafsson 1943
R. tardus W.C.R. Watson	28	Watson (Maude 1939)
R. tereticaulis P.J. Müll. subsp. *derasifolius* Sudre	28	Beijerinck 1956

Table 1. Continued.

Taxon	2*n*	References
R. ulmifolius Schott	14	Crane & Darlington 1927; Gustafsson 1933, 1939; Rozanova 1940; Heslop-Harrison 1953; Beijerinck 1956; Haskell 1960; Haskell & Tun 1961; Thompson 1995a
R. rusticanus Mercier	14	Datta 1932; Crane 1935; Thomas 1940a
R. ulmifolius Schott var. *inermis* (Willd.) Focke	14	Haskell & Tun 1961; Thompson 1995a
R. rusticanus Mercier var. *inermis*	14	Crane & Darlington 1927; Crane 1935
R. inermis Willd. cv. Burbank Thornless	14	Darrow & Longley 1933
R. vestervicensis Gust.	35	Gustafsson 1939, 1943
R. vestitus Weihe	28	Gustafsson 1939, 1943; Christen 1950; Beijerinck 1956
R. vigorosus P.J. Müll. & Wirtg.	28	Iwatsubo et al. 1995
R. affinis Weihe & Nees pro parte	28	Gustafsson 1933, 1939, 1943; Fabergé (Maude 1939); Heslop-Harrison 1953; Beijerinck 1956; Spies & DuPlessis 1985; Spies et al. 1985
R. villicauliformis A. Newton (as *R. villicaulis* Köhler. agg.)	28	Datta 1932
R. winteri P.J. Müll. ex Focke	28	Fabergé (Maude 1939)
R. wolley-dodii (Sudre) W.C.R. Watson	28	Heslop-Harrison 1953
Section *Rubus* (Doubtful determinations and/or taxonomic status)		
R. acutipetalus Lefèvre & P.J. Müll. (as *R. newbouldii* Bab.)	28	Harrison (Maude 1939)
R. adenolobus W.C.R. Watson (nom. nud.)	28	Heslop-Harrison 1953
R. alterniflorus P.J. Müll. & Lefèvre	28	Heslop-Harrison 1953
R. angustifrons Sudre	28	Heslop-Harrison 1953
R. apiculatus Weihe	28	Harrison (Maude 1939); Heslop-Harrison 1953; Beijerinck 1956; Markova 1968
R. apricus Wimm. var. *sparsipilus* W.C.R. Watson (nom. infaustum)	28	Heslop-Harrison 1953
R. aspericaulis Lefèvre & P.J. Müll.	28	Heslop-Harrison 1953
R. axillaris P.J. Müll. (nom. illeg.)	28	Harrison (Maude 1939)
R. caflischii Focke (uncertain determination)	28	Gustafsson 1943
R. chloocladus W.C.R. Watson *R. pubescens* Weihe	28	Gustafsson 1939
R. chlorothyrsus Focke	28	Heslop-Harrison 1953
R. concolor Ley	28	Heslop-Harrison 1953
R. cordifolius Blox.	28	Harrison (Maude 1939)
R. cordifolius Weihe & Nees	35	Gustafsson 1939
R. cuspidiferus (P.J. Müll. & Lefèvre) Boulay (as *R. cuspidifer* P.J. Müll. & Lefèvre)	28	Heslop-Harrison 1953

Table 1. Continued.

Taxon	2*n*	References
R. dasyphylloides (uncertain tax.)	49	Haskell 1960
R. drymophilus P.J. Müll. & Lefèvre	28	Heslop-Harrison 1953
R. fragrans Focke	42	Haskell 1960
R. fruticosus L. agg.	28	Marks 1952; Baquar & Askari 1970
R. fuscoater Weihe	28	Fabergé (Maude 1939)
R. fuscus Weihe	28	Marks 1952; Beijerinck 1956
R. genevierii Boreau	28	Gustafsson 1933, 1939
R. granulatus Lefèvre & P.J. Müll.	28	Heslop-Harrison 1953
R. hirtus Waldst. & Kit. agg.	28	Gustafsson 1933, 1939, 1943; Harrison (Maude 1939); Heslop-Harrison 1953; Boratynska 1995; Thompson 1995a
R. hirtus Waldst. & Kit. subsp. *kaltenbachii* Metsch var. *kaltenbachii*	28	Beijerinck 1956
R. horridisepalus (Sudre) W.C.R. Watson	28	Fabergé (Maude 1939)
R. hystrix Weihe	28	Heslop-Harrison 1953
R. insectifolius Lefèvre & P.J. Müll.	28	Heslop-Harrison 1953
R. insericatus P.J. Müll. ex Wirtg.	28	Heslop-Harrison 1953
R. integribasis P.J. Müll. ex Boulay	42	Heslop-Harrison 1953
R. kaltenbachii Metsch (uncertain tax.)	28	Gustafsson 1933, 1939
R. lejeunei Weihe	35	Heslop-Harrison 1953
R. leptadenes Sudre	28	Heslop-Harrison 1953
R. macrophylloides Genev.	28	Fabergé (Maude 1939)
R. macrostachys P.J. Müll.	28	Gustafsson 1943
R. magnificus P.J. Müll. ex Genev. (garden form)	42	Marks 1952; Heslop-Harrison 1953
as *R. borreri* Bell-Salt. (garden form)	42	Crane 1935; Thomas 1940a
as *R. borreri* Bell-Salt.	28	Fabergé (Maude 1939)
R. melanoxylon P.J. Müll. & Wirtg. (as *R. leyanus* W.M. Rogers)	28	Fabergé (Maude 1939)
R. mercieri Genev. (local biotype)	21	Christen 1950; Berger 1953
R. nitidus Weihe & Nees subsp. *opacus* Focke	28	Datta 1932
R. obcuneatus Lefèvre & P.J. Müll. (as *R. cenomanensis* Sudre)	35	Heslop-Harrison 1953
R. obscurissimus (Sudre) W.C.R. Watson	28	Harrison (Maude 1939)
R. obscurissimus (Sudre) W.C.R. Watson var. *pallidistaminus*	28	Heslop-Harrison 1953
R. obscurissimus (Sudre) W.C.R. Watson var. *pallidistaminus*	42	Harrison (Maude 1939)
R. obscurus Kaltenb.	28	Harrison (Maude 1939)
R. pedatifolius Genev. (uncertain tax.) *R. clethrophilus* P.J. Müll. (= Genev.?)	28	Heslop-Harrison 1953 Gustafsson 1933, 1939

Table 1. Continued.

Taxon	2*n*	References
R. plinthostylus Genev. (as *R. ornatus* Sudre)	28	Harrison (Maude 1939)
R. podophyllus P.J. Müll.	28	Heslop-Harrison 1953
R. pygmaeopsis Focke (as *R. koehleri* Weihe)	28	Harrison (Maude 1939)
R. rhamnifolius Weihe & Nees	21	Gustafsson 1943
R. rivularis P.J. Müll. & Wirtg.	28	Beijerinck 1956; Markova 1968
R. rotundellus Sudre	42	Harrison (Maude 1930)
R. scabrosus P.J. Müll.	35	Heslop-Harrison 1953
R. schleicheri Weihe ex Tratt.	28	Harrison (Maude 1939)
R. schmidelyanus Sudre var. *longiglandulosus* Sudre	35	Heslop-Harrison 1953
R. semipyramidalis Sudre (uncertain tax.)	35	Heslop-Harrison 1953
R. serpens Weihe ex Lej.	28	Beijerinck 1956
R. serpens Weihe ex Lej. & Courtois f. *arenarius*	28	Allander (Gustafsson 1943)
R. silesiacus Weihe	28	Heslop-Harrison 1953
R. sylvicolus Lefèvre & P.J. Müll.	28	Heslop-Harrison 1953
R. thyrsanthus Focke	28	Heslop-Harrison 1953
R. thysiflorus Weihe	28	Weihe (Maude 1939); Heslop-Harrison 1953
R. ulmifolius Schott var. *heteromorphus* (Ripart) Sudre	28	Heslop-Harrison 1953
R. uncinatiformis Sudre		
R. uncinatus P.J. Müll.	28	Harrison (Maude 1939)
R. vallisparsus Sudre	28	Harrison (Maude 1939); Heslop-Harrison 1953
R. vulgaris Weihe & Nees var. *mollis* Weihe & Nees	21	Heslop-Harrison 1953
Section *Corylifolii* Lindl.		
R. adenoleucus Chab.	35	Heslop-Harrison 1953
R. aureolus Allander	28	Allander 1941; Gustafsson 1943
R. aureolus Allander f. *suberiocarpus* Gust.	28	Gustafsson 1943
R. aureolus Allander var. *subglandulosus* A.A.W. Lund	28	Gustafsson 1943
R. nemorosus sensu Arrh., non Hayne & Willd.	28	Gustafsson 1933, 1939
R. nemorosus sensu Arrh. var. *suberiocarpus* ad int.	28	Gustafsson 1939
R. nemorosus sensu Arrh. var. *subglandulosus* Lund	28	Gustafsson 1939
R. babingtonianus W.C.R. Watson	28	Heslop-Harrison 1953
R. britannicus W.M. Rogers	42	Heslop-Harrison 1953
R. calvus H.E. Weber	28	Iwatsubo et al. 1995

Table 1. Continued.

Taxon	2*n*	References
R. camptostachys G. Braun		
R. divergens Neuman	42	Gustafsson 1933
R. ciliatus Lindeb.	28	Gustafsson 1939
R. ciliatus Lindeb.	±30	Gustafsson 1939
R. ciliatus Lindeb. var. *tiliaceus* (Aresch.) Gust.	28	Gustafsson 1943 (erroneously given as 42 in Gustafsson 1939)
R. conjungens (Bab.) W.M. Rogers	28	Heslop-Harrison 1953
R. conjungens (Bab.) W.M. Rogers	35	Heslop-Harrison 1953
R. purpureicaulis W.C.R. Watson	35	Heslop-Harrison 1953
R. contractipes H.E. Weber	28	Iwatsubo et al. 1995
R. cyclomorphus H.E. Weber		
R. cyclophyllus Lindeb.	42	Gustafsson 1939
R. demissus H.E. Weber & Martensen	28	Iwatsubo et al. 1995
R. dissimulans Lindeb. var. *bahusiensis* (Scheutz) Gust.	28	Gustafsson 1943 (erroneously given as 42 in Gustafsson 1933)
R. dissimulans Lindeb. var. *selectus* Frid.	42	Gustafsson 1939, 1943
R. dissimulans Lindeb. var. *suberectiformis* (Neuman) Gust.	28	Gustafsson 1939
R. dissimulans Lindeb. f. *ferox* (Frid.) Erichsen		
R. ferox Frid.	±42	Gustafsson 1939
R. nitens (Lindeb.) Neuman	42	Gustafsson 1933
R. dollnensis Sprib.	28	Boratynska 1994
R. eluxatus Neuman	28	Gustafsson 1943
R. centiformis Frid. pro parte	28	Gustafsson 1939
R. eluxatus Neuman ad *subnitidus* vergens	±28	Gustafsson 1939
R. eluxatus Neuman f. *subnitidus* Lidf.	28	Gustafsson 1939
R. eluxatus Neuman f. *subnitidus* Lidf.	45	Gustafsson 1933
R. fasciculatus P.J. Müll.	42	Gustafsson 1939
R. ambifarius P.J. Müll.	28	Gustafsson 1939, 1943
R. ambifarius P.J. Müll.	35	Gustafsson 1939
R. permixtus (Aresch.) A. Gust.	28	Gustafsson 1939
R. permixtus (Aresch.) A. Gust.	28–29	Gustafsson 1943
R. ferocior H.E. Weber	28	Iwatsubo et al. 1995
R. fioniae Frid. ex Neuman	28	Gustafsson 1939
R. glauciformis Gust. ex H. Hyl.	28	Gustafsson 1943
(*R. caesius* × *wahlbergii*) f. *glauciformis* Gust.	28	Gustafsson 1939

Table 1. Continued.

Taxon	2*n*	References
R. gothicus Frid. & Gelert ex E.H.L. Krause	28	Gustafsson 1939, 1943
R. gothicus Frid. & Gelert ex E.H.L. Krause	±28	Gustafsson 1939
R. acuminatus Lindeb.	28	Gustafsson 1933
R. gothicus Frid. & Gelert ex E.H.L. Krause	35	Gustafsson 1939
R. gothicus Frid. & Gelert ex E.H.L. Krause f. *microphylla*	28	Gustafsson 1939
R. gothicus Frid. & Gelert ex E.H.L. Krause f. *umbrosa*	28	Gustafsson 1943
R. grossus H.E. Weber	35	Boratynska 1994
R. hallandicus (Gabr. ex Aresch.) Neuman	28	Gustafsson 1939, 1943
R. halsteadensis W.C.R. Watson		
R. raduliformis (Ley) W.C.R. Watson	35	Heslop-Harrison 1953
R. hystricopsis (Frid.) A. Gust.	28	Gustafsson 1939
R. lagerbergii Lindeb.	35	Gustafsson 1943
R. lamprocaulos G. Braun	28	Iwatsubo et al. 1995
R. serrulatus Lindeb. f. *eglandulosa* Gust.	28	Gustafsson 1943
R. serrulatus Lindeb. f. *ditior* Frid.	28	Gustafsson 1939
R. lidforssii (Gelert) Lange		
R. centiformis var. *lidforssii* (Gelert) A. Gust.	28–35	Gustafsson 1939
R. centiformis var. *lidforssii* (Gelert) A. Gust.	28	Gustafsson 1939
R. lindbloomii Westerl.		
R. centiformis Frid. var. *mortensenii* Frid. & Gelert	28	Gustafsson 1939
R. centiformis Frid. var. *mortensenii* Frid. & Gelert	42	Gustafsson 1939
R. nemorosus Hayne & Willd.	28	Iwatsubo et al. 1995
R. balfourianus A. Bloxam ex Bab.	28	Heslop-Harrison 1953
R. balfourianus A. Bloxam ex Bab.	35	Heslop-Harrison 1953
R. norvegicus H.E. Weber & Pedersen		
R. rosanthus Lindeb. var. *lejocarpus* Lindeb.	28	Gustafsson 1939, 1943
R. rosanthus Lindeb. var. *lejocarpus* Lindeb.	35	Gustafsson 1943
R. rosanthus Lindeb. var. *lejocarpus* Lindeb.	49	Gustafsson 1939
R. orthostachys G. Braun	28	Boratynska 1994
R. phylloglota (Frid.) A. Gust.	28	Gustafsson 1939
R. pruinosus Arrh. f. *pruinosus*	35	Gustafsson 1939
R. sublustris Lees	35	Heslop-Harrison 1953
R. pruinosus Arrh. var. *silvaticus* Gust. ad int.	35	Gustafsson 1939
R. pruinosus Arrh. f. *warmingii* (Jensen ex Neuman) H.E. Weber		
R. pruinosus Arrh. var. *opimus* A.A.W. Lund	35	Gustafsson 1943
R. pruinosus Arrh. var. *warmingii* (Jensen ex Neuman) Gust. ex A. Gust.	35	Gustafsson 1939, 1943

Table 1. Continued.

Taxon	2*n*	References
R. rhytidophyllus H.E. Weber	28	Iwatsubo et al. 1995
R. rosanthus Lindeb. var. *eriocarpus* Lindeb.	35	Gustafsson 1939
R. slesvicensis Lange	42	Thompson 1995a
R. suecius H.E. Weber & Karlsson		
R. fioniae Frid. var. *benefixus* Gust.	28	Gustafsson 1943
R. tiliaster H.E. Weber		
R. tileaceus Lange	42	Gustafsson 1933
R. tuberculatus Bab.	35	Heslop-Harrison 1953
R. myriacanthus auct.	35	Heslop-Harrison 1953
R. wahlbergii Arrh.	35	Gustafsson 1939, 1943; Thompson 1995a
R. wahlbergii Arrh. var. *magnificus* Frid.	35	Gustafsson 1939
R. wahlbergii Arrh. var. *partitus* Gust.	35	Gustafsson 1939
R. wahlbergii Arrh. f. *umbrosa*	35	Gustafsson 1939
R. insulariformis (local form of walhlbergii?)	42	Gustafsson 1933
R. warrenii Sudre	28	Heslop-Harrison 1953
Section *Corylifolii* (Doubtful determinations and/or taxonomic status)		
R. acutus Lindeb. nom. illeg.; non *acutus* Braeucker	42	Gustafsson 1939
R. acutus Lindeb. var. *fioniaeformis* Newman	28	Gustafsson 1943
R. acutus Lindeb. var. *nemorosiformis* Neuman	28	Gustafsson 1943
R. acutus Lindeb. var. *ruedensis* (Lidf.)	42	Gustafsson 1939
R. acutus Lindeb. var. *progenerans* (Lidf.)?	42	Gustafsson 1939
R. adenoleucus Chab.	35	Heslop-Harrison 1953
R. corylifolius Sm. agg.	28	Longley 1924
R. corylifolius Sm. agg.	35	Datta 1932
R. dumetorum Weihe	35	Marks 1952
R. galbidus Kan.	28	Gustafsson 1943
R. internatus Gust. ex H. Hyl.		
R. ruderalis Aresch. (local biotype)	±30	Gustafsson 1939
R. maximus (L. ex Aresch.) Neuman, non *maximus* T. Marsson (nom. illeg.-local biotype)		
R. balticus Aresch.	49	Gustafsson 1939
R. lagerbergii Lindeb. var. *balticus* Aresch.	49	Gustafsson 1933
R. lagerbergii Lindeb. var. *balticus* (Aresch.) Frid.	35/2	Gustafsson 1943
R. lagerbergii Lindeb. var. *balticus* (Aresch.) Frid.	70?	Gustafsson 1943 (given as $n = 35$)
R. ostenfeldii Frid. (vars. represent limited local forms)		
R. ostenfeldii Frid. var. *micrander* Frid.	28	Gustafsson 1939
R. ostenfeldii Frid. var. versus *warmingii*	42	Gustafsson 1939

Table 1. *Continued.*

Taxon	2*n*	References
R. ostenfeldii Frid. var. versus *warmingii*	±44	Gustafsson 1939
R. olavii Neuman f. (invalid name)	±42	Gustafsson 1939
R. rotundellus Sudre	42	Harrison (Maude 1939)
R. scabrosus Focke	35	Heslop-Harrison 1953
R. trivultus Frid. f. *kullensis*	28	Gustafsson 1933
R. umbelliformis P.J. Müll. & Lefèvre	35	Heslop-Harrison 1953
R. vexatus Frid. (local biotype)		
R. vexatus Frid. var. *crispus* Frid.	42	Gustafsson 1939
Section *Caesii* Lej. & Courtois		
R. caesius L.	28	Longley 1924; Datta 1932; Gustafsson 1933, 1939, 1943; Rozanova 1934, 1940; Rohweder 1937; Vaarama 1939; Christen 1950; Berger 1953; Beijerinck 1956; Haskell 1960; Haskell & Tun 1961; Engelskjon 1979; Boratynska 1995; Thompson 1995a
R. caesius L. var. *turkestanicus* Regel	28	Longley 1924; Rozanova 1934, 1940
Subgenus *Rubus* (North American blackberry species)		
Section *Allegheniensis*		
R. allegheniensis Porter	14	Longley 1924; Einset 1947; Einset & Pratt 1954; Aalders & Hall 1966
R. villosus American authors non Aiton	14	Longley 1924
R. allegheniensis Porter	21	Longley 1924; Einset 1947
R. avipes L.H. Bailey	21	Einset 1947
R. pergratus Blanch.	21	Longley 1924
R. sativus Brainerd (pro parte)	21	Longley 1924
R. alumnus L.H. Bailey		
R. bellobatus L.H. Bailey	21	Einset 1947
R. bellobatus L.H. Bailey	28	Einset 1947
R. pugnax L.H. Bailey	14	Einset 1947
R. rosa L.H. Bailey	21	Einset 1947
Section *Arguti*		
R. abactus L.H. Bailey	35	Einset 1947
R. amnicolus Blanch.	21	Longley 1924
R. andrewsianus Blanch.	21	Longley 1924
R. argutus Link	14	Longley 1924
R. argutus Link	21	Longley 1924
R. floridus Tratt. cv. Early Harvest	14	Fischer et al. 1941

Table 1. Continued.

Taxon	2*n*	References
R. frondosus Bigelow	14	Longley 1924
R. frondosus Bigelow	21	Longley 1924
R. frondosus Bigelow	42	Longley 1924
R. louisianus A. Berger	14	Markarian & Olmo 1959
R. orarius Blanch.	21	Longley 1924
R. pensilvanicus Poir.	28	Einset 1947
R. recurvans Blanch.	21	Longley 1924
R. cardianus L.H. Bailey (syn.?)	35	Einset 1947
R. recurvans Blanch.		
R. wiegandii L.H. Bailey	36	Einset 1947
R. recurvans Blanch.	42	Longley 1924
R. uniquus L.H. Bailey	28	Einset 1947
R. uvidus L.H. Bailey		
R. localis L.H. Bailey	21	Einset 1947
Section *Canadenses*		
R. canadensis L.	14	Longley 1924; Thompson 1995a
R. randii Rydb.	14	Longley 1924
R. canadensis L.	21	Longley 1924; Einset 1947; Craig 1960; Thompson 1995a
Section *Cuneifolii*		
R. cuneifolius Pursh	14	Sharpe & Shoemaker 1958; Shoemaker & Sturrock 1959; Sherman 1968; Spies & DuPlessis 1985; Spies et al. 1985
R. cuneifolius Pursh	21	Spies & DuPlessis 1985; Spies et al. 1985
R. cuneifolius Pursh	28	Spies & DuPlessis 1985; Spies et al. 1985
R. pascuus L.H. Bailey	21	Spies & DuPlessis 1985; Spies et al. 1985
R. pascuus L.H. Bailey	28	Spies & DuPlessis 1985; Spies et al. 1985
R. serissimus L.H. Bailey	28	Einset 1947
Section *Flagellares*		
R. aboriginum Rydb. cvs. Austin Dew, Austin Thornless, and Austin Mayes	56	Thompson 1961
R. arundelanus Blanch.	42	Longley 1924
R. jeckylanus Blanch.	42	Longley 1924
R. biformispinus Blanch.	21	Longley 1924
R. flagellaris Willd.	28	Spies & DuPlessis 1985; Spies et al. 1985
R. villosus Aiton	35	Longley 1924
R. geophilus Blanchard	49	Einset 1951
R. flagellaris Willd.	56	Faasen & Nadeau 1976

Table 1. Continued.

Taxon	2*n*	References
R. flagellaris Willd.	63	Einset 1947
R. meracus L.H. Bailey	49	Einset 1947
R. multiformis Blanch.	21	Longley 1924
R. noveboracus L.H. Bailey	35	Einset 1947
R. plicatifolius Blanch.	35	Longley 1924
R. plicatifolius Blanch, *R. semierectus* Blanch.	42	Longley 1924
R. recurvicaulis Blanch.	14	Longley 1924
R. roribaccus (L.H. Bailey) Rydb. (as *R. flagellaris*, in part, cv. Lucretia)	49	Thompson 1961
R. satis L.H. Bailey (as *R. plicatifolius* Blanch.)	63	Einset 1947
Section *Hispidi*		
R. hispidus L.	14	Aalders & Hall 1966; Thompson 1995a
R. hispidus L.	35	Longley 1924
R. hispidus-like	56	Longley 1924
R. huttonii L.H. Bailey	28	Einset 1947
R. plus L.H. Bailey	21	Einset 1947
R. signatus L.H. Bailey	21	Einset 1947
R. tardatus Blanch.	21	Longley 1924
Section *Setosi*		
R. clandestinus L.H. Bailey *R. jejunus* L.H. Bailey	28	Einset 1947
R. dissensus L.H. Bailey	21	Einset 1947
R. glandicaulis Blanch.	21	Longley 1924
R. hanesii L.H. Bailey	28	Einset 1947
R. miscix L.H. Bailey *R. peculiaris* Blanch.	21	Longley 1924
R. notatus L.H. Bailey *R. bootianus* L.H. Bailey	14	Einset 1947
R. setosus Bigelow	14	Longley 1924
R. setosus Bigelow *R. nigricans* Rydb.	21	Longley 1924

Table 1. Continued.

Taxon	2*n*	References
R. wisconsinensis L.H. Bailey		
R. minnesotanus L.H. Bailey	35	Einset 1947
Section *Verotriviales*		
R. trivialis Michx.	14	Yarnell 1936; Sharpe & Shoemaker 1958; Shoemaker & Sturrock 1959; Sherman 1968; Thompson 1995a, b
R. rubrisetus Rydb.	14	Yarnell 1932
Section *Ursini*		
R. ursinus Cham. & Schltdl.	42	Fischer et al. 1941; Brown 1943; Vaarama 1953
R. loganobaccus L.H. Bailey	42	Darrow & Longley 1933; Thomas 1940a, b; Vaarama 1953
R. ursinus Cham. & Schltdl.	56	Darrow & Longley 1933; Fischer et al. 1941; Brown 1943; Zielinski & Galey 1951; Vaarama 1953; Thompson 1961; Thompson 1995b
R. vitifolius Cham. & Schltdl.	56	Thomas 1940a, b
R. ursinus Cham. & Schltdl.	63	Brown 1943
R. ursinus Cham. & Schltdl.	70	Darrow & Longley 1933; Brown 1943; Vaarama 1953; Thompson 1961
R. ursinus Cham. & Schltdl.	77	Brown 1943
R. ursinus Cham. & Schltdl.	84	Darrow & Longley 1933; Fischer et al. 1941; Brown 1943; Gustafsson 1943; Iwatsubo & Naruhashi 1993; Thompson 1995a, b
R. macropetalus Douglas	84	Darrow & Longley 1933; Zielinski & Galey 1951
Subgenus *Rubus* (South American blackberry species)		
Section *Floribundi*		
R. adenotrichos Schltdl.	14	Thompson 1995a
R. bogotensis Kunth	14	Gustafsson 1939; Dale & Ingram 1981
R. robustus C. Presl	14	Thompson 1995a
R. uticifolius Poir.	14	Thompson 1995a
Proposed Natural Inter-Subgeneric Hybrid		
R. glaucus Benth. (*Rubus* × *Idaeobatus* ?)	28	Williams et al. 1949; Dale & Ingram 1981; Thompson 1995a